

Salinity Sensitivity of Sorghum at Three Growth Stages

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Summary. The relative salt tolerance of two sorghum cultivars [Sorghum bicolor (L.) Moench., cvs. Northrup King 265 and Asgrow Double TX] at three different stages of growth was determined in a greenhouse experiment. Plants were grown in sand cultures irrigated four times daily with modified Hoagland's solution. A nonsaline solution and six solutions salinized with NaCl and CaCl₂ (2:1 molar ratio) provided treatments with osmotic potentials (ψ_s) ranging from -0.05 to -1.05 MPa. The saline treatments were imposed for 30 days beginning at either Stage 1, 4, or 7 as defined by Vanderlip and Reeves (Agron J. 64:13, 1972). The 30-day stages are referred to here as the vegetative, reproductive and maturation stages although the first stage may have included initial panicle differentiation. Both cultivars were most sensitive to salinity during the vegetative stage and least sensitive during maturation. Based on a nonlinear leastsquares analysis, grain yield reductions of 50% were predicted at $\psi_s = -0.68$, -1.02, and -1.14 MPa for NK 265 and at -0.62, -1.00, and -1.10 MPa for Double TX when salinized during the vegetative, reproductive, and maturation stages, respectively. Although salinity had no significant effect on mean kernel weights, significant growth stage effects and interaction indicated that kernels were heaviest for plants salinized during the vegetative stage. Stover yields were significantly reduced by salination during the vegetative stage but were unaffected when plants were salinized during the maturation stage. Salination during the reproductive stage also decreased stover yield of Double TX but the effect was smaller than that during the first stage. Stover yield of NK 265 was unaffected by salinity at this stage.

Mineral analysis of the first leaf below the flag leaf at harvest indicated that both cultivars tended to exclude Na from the upper leaves. Ca and Cl concentrations increased with increased salinity in plants salinized during the maturation stage but salination in earlier stages decreased Ca concentration of this upper leaf at harvest and had no effect on the final Cl concentration. Phosphate and K concentrations decreased when plants were salinized during the third stage but increased when plants were salinized during the vegetative and reproductive stages. Mg was unaffected by salinization during the first and last stage but decreased when plants were salinized during the reproductive stage.

An extensive data base now exists which describes the salt tolerances of many different crops (Maas and Hoffman 1977; Maas 1986). These data express yield responses as a function of the average salt concentration in the rootzone. Generally, these data apply only if salinity is fairly uniform from the seedling stage to maturity. Except for germination, little information exists on the tolerances of crops at different stages of growth. Such information could be invaluable to optimize the use of limited water resources. Knowledge that crops are more tolerant during some stages of growth will improve new strategies for utilizing saline drainage waters (Rhoades 1984).

Several studies indicate that tolerances do change as the crop develops and matures, but none of these studies completely separated the effects of duration of treatment from the stage of growth that the crop was treated (Ayers et al. 1952; Kaddah and Ghowail 1964; Kovalskaia 1958; Lunin et al. 1961a, 1961b; Maas et al. 1983; Ogo and Sasai 1955; Piruzyan 1959; Verma and Bains 1974). Comparisons of sensitivity during specific phenological stages are confounded when treatment periods are of unequal duration.

This study was initiated to determine the sensitivity of grain sorghum [Sorghum bicolor (L.) Moench] to salinity during three 30-day periods of growth. Francois et al. (1984) recently reported that sorghum is a moderately salt-tolerant crop. In field plot tests, grain yields of two cultivars decreased 16% per unit increase in salinity (electrical conductivity of saturated soil extracts from the rootzone) above 6.8 dS/m. They further reported that both cultivars were significantly more tolerant at germination than at later stages of growth. Soil water salinities above 8.2 dS/m delayed germination but full germination occurred within 10 days at salinities up to 22 dS/m. Treatments in the present study were designed to assess plant growth and yield responses to 30-day exposures to salinity beginning at either the 2-leaf stage, at the beginning of rapid culm elongation, or after anthesis.

Experimental Procedures

Two sorghum cultivars, Northrup King 265 ¹ and Asgrow Double TX, were grown in sand cultures in a greenhouse. The sand cultures consisted of 60 tanks (1.2 m × 0.6 m × 0.5 m deep) filled with washed sand. The sand had an average bulk density of 1.2 Mg m⁻³ and an average volumetric water content of 0.34 m³/m³ at saturation. Two rows of each cultivar (25 seeds per row) were planted in each sand tank on July 11, 1983. Plants were later thinned to 17 plants per row. The plants were irrigated four times daily with a modified Hoagland nutrient solution consisting of 2.5 mM Ca (NO₃)₂, 3.0 mM KNO₃, 0.17 mM KH₂PO₄, 1.5 mM MgSO₄, 100 μM Fe as sodium ferric diethylenetriamine pentaacetate, 23 μM H₃BO₃, 5 μM MnSO₄, 0.4 μM ZnSO₄, 0.2 μM CuSO₄, and 0.1 μM H₂MoO₄ added to Riverside tap water. Each irrigation was applied for approximately 15 min until the sand was completely saturated after which the nutrient solution drained into 565-liter reservoirs for subsequent use in the next irrigation. The solutions were salinized by adding NaCl and CaCl₂ at a 2:1 molar ratio. The pH of the irrigation solution was maintained between 6.0–6.5. Air temperatures ranged from 17–38 °C with a mean tem-

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perature of 28 °C throughout the course of the experiment. Relative humidity ranged from 32–100% with a mean of 67%.

The experimental design was a randomized block factorial consisting of six salinity treatments with osmotic potentials (ψ_s) of -0.25, -0.35, -0.45, -0.65, -0.85, and -1.05 MPa applied during three growth stages each replicated three times. A control treatment maintained at -0.05 MPa during all stages was replicated six times. To insure a full and uniform plant stand, salination of the first stage began seven days after seeding and continued until Day 36. Salination during the second stage was imposed from Day 37 to Day 66. Third stage salination began after anthesis on Day 67 and continued until harvest on Day 98. All plants were irrigated with nonsaline nutrient solution when not on saline treatments. These three growth stages are referred to in this paper as the vegetative, reproductive, and maturation treatment periods, respectively. They correspond approximately to those described by Vanderlip and Reeves (1972); the vegetative treatment period corresponded to Stages 1–3, the reproductive period to Stages 4–6, and the maturation period to Stages 7–9.

To minimize osmotic shock during salination, the ψ_s of the irrigation solution was decreased 0.2 MPa per day split equally between morning and afternoon. Water lost by evapotranspiration was added to the reservoirs each day to prevent the solution from concentrating. The desalination rate at the end of the treatment periods was approximately 0.2 MPa per irrigation. All nutrient solutions were replaced with fresh solution at the beginning of the second and third stages.

An infestation of spider mites was controlled by applying Vendex at a rate of 4.5 kg ha⁻¹ at 60, 65, and 84 days.

On Day 95 the first leaf below the flag leaf was sampled on random plants in every tank and composite samples were dried and ground for mineral analysis. Na, K, Ca, and Mg were determined on nitric-perchloric acid digests by atomic absorption spectrophotometry. Chloride was determined on dilute acetic and nitric acid extracts by coulometric-amperometric titration (Cotlove 1963).

To determine if the salinity treatments had any effect on pollen viability, selected sorghum heads in each treatment were covered with paper bags as soon as they emerged from the boot and then were uncovered near the end of the experiment.

At 98 days all plants were fully mature except for those treated with -0.85 and -1.05 MPa during the vegetative stage which were harvested 23 days later. The mature plants were harvested and fresh weights of heads and stover were obtained. Grain and stover were ovendried at $60\,^{\circ}\text{C}$ and dry weights of stover, grain, and 100-seed lots were obtained.

Statistical analyses included analysis of variance, nonlinear least-squares techniques, and pairwise comparison based on Student's *t*-distribution.

Results and Discussion

Plant Growth

Although salinity significantly decreased plant height during the vegetative stage for both cultivars, the plants recovered considerably during the following stage (Ta-

ble 1). Plants that were 76 to 82% smaller at 38 days were only 21 to 29% smaller at 67 days (NK 265 and DTX at -1.05 MPa, respectively). Similar reductions in height occurred when salinity was imposed during the second stage of growth. The decrease in plant height at both stages was a linear function of the ψ_s . Salination at the third stage had no effect on plant height since the plants were fully grown when the treatment was imposed. Salinity during the second stage reduced stem elongation but had less effect on plant height than salinity imposed during the vegetative stage where it resulted in decreased leaf elongation.

Salination during the vegetative stage delayed booting. This effect was most pronounced in the -0.85 MPa and -1.05 MPa treatments where booting was delayed approximately 8 days. Subsequent development was also retarded which delayed the harvest date 23 days for those two treatments. Sorghum heads that were covered with paper bags to prevent pollination from nonsaline control plants were fully developed indicating salinity had no effect on pollen viability.

At ψ_s 's below -0.25 MPa, salinity caused leaf necrosis on plants salinized during the reproductive and maturation stages. Salination during the maturation stage caused substantial leaf senescence and necrosis. The symptoms appeared on older leaves approximately one week after salination began and with decreased ψ_s , increasingly younger tissues were affected. This salt-induced necrosis was not observed on plants salinized during the vegetative stage.

Grain Yield

Grain yields were greatly decreased by salinity and the decreases differed depending upon the stage of growth the crop was salinized (Table 2). Both effects were highly significant. The probabilities of an interaction between the growth stage that salt was applied and salinity were 0.065 and 0.10 for NK 265 and DTX, respectively. Total grain yield per plant was decreased most by salination during the vegetative stage and least during the grain maturation stage. The effect of salinity on yield during the reproductive stage was intermediate. Although moderate salinity levels increased grain yields in some cases, Student's *t*-test comparisons with the controls indicated that these increases were not significant $(P \le 0.05)$.

Recently, van Genuchten and Hoffman (1984) have described a nonlinear least-squares inversion method to analyze crop salt tolerance data. A computer program developed by van Genuchten (1983) provides 20 different options to determine the "best-fit" response curve depending upon the particular salt tolerance model chosen and the type and number of unknown parameters to be estimated. Because of a significant replication effect, our data were analyzed with NOPT=14 which determines a normalized yield response function. In this model,

$$\frac{1}{1 + \left(\frac{c}{c_{50}}\right)^{p}}$$

where Y_r is the relative yield, c is the ψ_s , C_{50} is the ψ_s corresponding to a 50% yield reduction, and p is an empirical constant. Fig. 1 shows the fitted curves for the treatments of three growth stages for both sorghum cultivars. The analysis indicates

Table 1. Plant height at 38 and 67 days of sorghum cultivars NK 265 and Double TX as in
fluenced by salinity imposed during vegetative (V) and reproductive (R) stages of growth

Salinity treatment	NK 265			DTX			
	Day 38	Day 38 Day 67		Day 38	Day 67		
	V	V	R	V	$\overline{\mathbf{v}}$	R	
MPa				cm			
-0.05	101	129	129	109	143	143	
-0.25	93	120	115	89	137	136	
-0.35	74	122	101	82	139	124	
0.45	66	128	106	63	132	122	
-0.65	46	113	103	35	123	116	
-0.85	28	101	98	26	108	110	
-1.05	25	102	101	20	104	108	

Table 2. Grain yield of sorghum cultivars NK 265 and Double TX as influenced by salinity at the vegetative, reproductive and maturation stages of growth

Salinity	NK 265				DTX			
treatment	v	R	M		v	R	M	
MPa	,			g/plant				
-0.05	13.6	13.6	13.6		15.7	15.7	15.7	
-0.25	13.7	13.9	14.1		17.7	17.4	14.6	
-0.35	11.8	12.2	16.4		19.3	14.2	17.1	
-0.45	10.0	14.5	14.2		8.9	17.6	22.4	
-0.65	5.2	11.1	11.1 16.0		4.8	10.0	16.2	
0.85	4.0	10.1	10.1 11.8		4.4	9.2	13.7	
-1.05	4.6	5.8	9.7		6.1	7.6	11.3	
Source	df		Analysis of	variance				
			NK 265			DTX		
			F value	$P > F^a$		F value	<i>P</i> >F	
Rep	2		12.61	0.0001		15.78	0.000	
Salinity	6		9.16	0.0001		6.15	0.000	
Growth stage	2		14.09	0.0001		5.98	0.0053	
$S \times GS$	12		1.90	0.0649		1.71	0.1003	

^a Probability that a significant F value would occur by chance

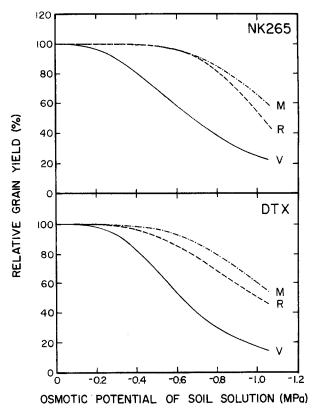


Fig. 1. Relative grain yields of two sorghum cultivars as a function of the osmotic potential of the soil solution imposed during three growth stages – vegetative, reproductive, and maturation

a clear increase in the C_{50} value the later salinity was imposed during the growth cycle. Based on this smooth curve option, values of C_{50} for NK 265 were -0.68, -1.02, and -1.14 MPa, and those of Double TX were -0.62, -1.00, -1.10 MPa for the vegetative, reproductive, and maturation stages, respectively. Values of p were 2.79, 6.27, and 4.94 for NK 265 and 3.46, 3.38, and 4.29 for Double TX, respectively.

Kernel Weight

Mean kernel weight was significantly affected by the stage of growth that salt stress was imposed, but not by increasing salinity up to -1.05 MPa (Table 3). However, the interaction between the level of salinity and the stage of growth the stress was imposed was significant for both cultivars. Kernel weights of both cultivars were highest for plants salinized during the vegetative stage. The heavier kernels resulting from the -0.85 and -1.05 MPa treatments imposed during the vegetative stage should be considered separately because of the 23-day delay in maturation of plants in these treatments.

Salinity treatment	NK 265			DTX			
	v	R	M	V	R	М	
MPa				g			
-0.05	2.83	2.83	2.83	2.16	2.16	2.16	
-0.25	2.99	2.01	2.74	2.42	2.13	1.88	
-0.35	3.16	2.03	2.60	2.21	1.42	2.00	
-0.45	3.25	2.16	2.68	2.53	1.58	1.82	
0.65	3.20	1.81	2.78	1.99	1.37	1.95	
-0.85	3.43	2.13	2.22	3.24	1.59	1.70	
1.05	3.37	2.47	1.70	3.12	1.91	1.47	

Table 3. Dry weight of 100-seed lots of sorghum cultivars NK 265 and Double TX as influenced by salinity at the vegetative, reproductive and maturation stages of growth

Source	df	Analysis of variance					
		NK 265		DTX			
		F value	$P > F^a$	F value	<i>P</i> >F		
Rep	2	0.66	0.5199	1.61	0.2126		
Salinity	6	0.89	0.5092	1.41	0.2342		
Growth stage	2	56.98	0.0001	22.46	0.0001		
$S \times GS$	12	3.29	0.0022	2.54	0.0135		

^a Probability that a significant F value would occur by chance

Stover Yield

Stover yields were significantly affected by both salinity and the growth stage it was imposed (Table 4). The interaction was also significant for both cultivars. As expected from plant height measurements, stover weights were reduced when salinity was imposed during the first stage but were not significantly affected when salinity was imposed during the third stage. The effect of salination during the reproductive stage was intermediate, although only the stover yield of Double TX was significantly decreased by salinity at this stage. During the 23-day delay while the plants treated at -0.85 and -1.05 MPa during Stage I were maturing, the plants in these two treatments grew significantly. This was particularily true of NK 265 as is apparent from the larger stover weights for these treatments (Table 4).

Mineral Composition

The Ca, Mg, Na, K, Cl, and P concentrations of the first leaf below the flag leaf sampled on day 95 are shown in Fig. 2. Most of the growth and expansion of this leaf occurred during the reproductive stage. Therefore, leaf mineral composition of plants exposed to salinity during the vegetative stage mainly reflects the nonsaline conditions of the second and third stages. Mineral composition of plants exposed to salinity during the reproductive stage reflects changes in an expanding leaf under saline conditions followed by nonsaline conditions during the third stage.

Table 4. Dry weight of stover of sorghum cultivars NK 265 and Double TX as influenced by salinity at the vegetative, reproductive and maturation stages of growth

Salinity	NK 265				DTX			
treatment	v	R	М		V	R	M	
MPa				g/plant				
-0.05	14.4	14.4	14.4		17.5	17.5	17.5	
-0.25	13.5	15.1	15.3		17.1	15.9	17.5	
-0.35	12.0	11.8	16.3		12.8	15.2	19.2	
-0.45	8.9	14.7	15.5		8.9	17.4	19.2	
-0.65	5.9	12.0	15.1		8.3	12.4	20.3	
-0.85	11.3	11.0	15.4		7.3	11.6	17.9	
-1.05	13.6	12.1	15.8		8.4	12.7	17.3	
Source	df		Analysis of	variance				
			NK 265		_	DTX		
			F value	$P > F^a$		F value	<i>P</i> >F	
Rep	2		7.39	0.0019		34.07	0.0001	
Salinity	6		2.39	0.0454		14.11	0.000	
Growth stage	2		13.98	0.0001		98.96	0.0001	
S×GS	12		2.14	0.0359		8.07	0.0001	

^a Probability that a significant F value would occur by chance

The ion concentrations of the salinizing salts, Na, Ca, and Cl, were highest in leaves of both cultivars salinized during the third stage. When salinity was imposed during the vegetative stage, Ca concentrations generally decreased as ψ_s 's decreased below -0.35 MPa. This residual effect of high salinity levels imposed during the vegetative stage on Ca accumulation by a leaf that developed later during nonsaline conditions was unexpected. A similar decrease in Ca concentration occurred in plants salinized during Stage 2. Apparently plants that were heavily salinized during one of the first two stages did not accumulate as much Ca during Stage 3 as control plants. Na, which was excluded from the upper leaves of both cultivars, tended to increase when plants were salinized during Stage 3 but the increase was minimal. Effects of salinity on Na concentrations during Stages 1 and 2 were also inconsequential. Cl concentrations increased markedly when plants were salinized during Stage 3 but were fairly uniform in plants exposed to increased salinity during the earlier stages. It is possible that the Cl that accummulated during Stage 2 was transported out of the leaf during the subsequent nonsaline stage. However, there is no evidence that Cl which presumably was accumulated by older leaves during first stage salinization, was transported to the younger analyzed-leaf during the subsequent stages.

Mg concentrations decreased with increased salinity imposed during Stage 2 but were unaffected by salination during Stage 1 and 3. This suggests that salt de-

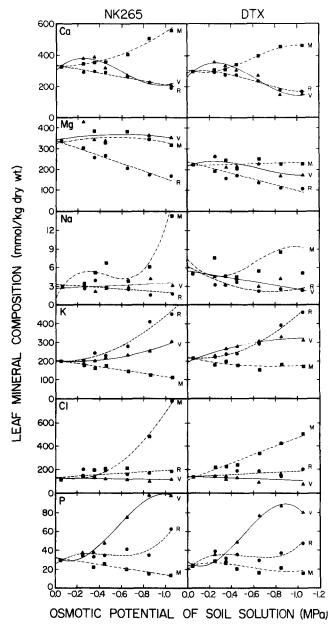


Fig. 2. Leaf mineral composition of two sorghum cultivars at harvest as a function of the osmotic potential of the soil solution imposed during three growth stages – vegetative, reproductive and maturation. Concentrations measured in first leaf below the flag leaf on Day 95

creased Mg uptake while the leaf was expanding and that little or no Mg uptake occurred during Stage 3 whether salt was present or not. Increased salinity during Stage 3 decreased K accumulation but concentrations increased significantly with increased salinity when imposed during the vegetative and especially the reproductive stage. The effect of increased salinity on P was similar except that leaf concentrations were greatest for plants exposed to salt during the vegetative stage. It is clear that these interactions between salt levels and growth stages on the accumulation of various ions will require periodic analyses throughout the growth cycle to explain the nature of these effects. Some increases in ion concentrations may reflect the concentrating effect of reduced shoot growth caused by salt stress. Other changes may be caused by direct effects of salt on ion uptake by the roots or on translocation to other organs.

Conclusion

The results of this study show that of the three growth stages studied, sorghum is most sensitive to salinity during the vegetative stage and least sensitive during the maturation stage. Although both cultivars recovered considerably after stress during the first stage was relieved, growth was substantially reduced. Since most of the vegetative growth occurred during the first stage, salinity had a lesser effect on stover yield when imposed during the second stage and no effect when imposed during the third stage. In fact, the detrimental effects of salinity on stover yields during the second stage were only significant for Double TX and not for NK 265. Grain yields were also decreased most by salt stress imposed during the first stage and least by stress imposed during the third stage. Since plants stressed during the first stage produced the heaviest kernels, the decrease in grain yield resulted from a substantial reduction in the number of seed per plant. This suggests that the first stage salination may have affected initial panicle differentiation. Vanderlip and Reeves (1972) point out that growing point differentiation occurs approximately 30 days after emergence. Emergence occurred on Day 3 in our experiment, and first stage salination continued until Day 36, therefore, if salinity did not delay panicle differentiation, it would have begun 3 days before the end of Stage 1. Whether salinity affects the onset of panicle differentiation will be tested in a separate experiment with close anatomical observation.

According to results cited by Krieg (1983), sorghum is most sensitive to water stress during the reproductive stage when seed number is reduced. It should be noted that the plants in this experiment were not exposed to any water stress. Potential water stress under nonsteady-state field conditions could exacerbate the effects of salt stress.

Chemical analyses of the second leaf from the top of the plant revealed several differential effects of salt stress when imposed at different growth stages on leaf mineral composition. Since leaves were not sampled periodically throughout the growth cycle, many of these interactions cannot be fully explained. It appears, however that Na is essentially excluded from the upper leaves of these sorghum cultivars despite high concentrations in the root media. Increased salt stress during Stage 3 increased Ca and Cl concentrations but earlier salination decreased the Ca

concentration of this upper leaf at harvest and had no effect on the final Cl concentration. K and P concentrations decreased only when stress was imposed during the maturation stage and Mg decreased only when salinized in the reproductive stage. Despite some substantial decreases in certain nutrient concentrations, no detrimental nutritional effects were apparent.

The practical implication of these results is that sorghum could be irrigated with poorer quality waters after flowering without reducing yields provided water of acceptable quality is used during vegetative and early reproductive growth.

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